Understanding the evolution of infidelity using the Seychelles warbler system

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Chapter 4

Heritability of female infidelity in the Seychelles warbler

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A white-tailed tropicbird flies over Cousin (photo by Martijn Hammers).

4.1. Abstract

Extra-pair paternity is widespread across socially monogamous taxa, yet the evolutionary drivers of infidelity remain elusive. Given that, unlike in males, infidelity does not necessarily increase reproductive success in females, it is unclear why females would engage in extra-pair mating. One influential hypothesis (the 'good genes' hypothesis) maintains that female infidelity evolved under selection acting through indirect additive genetic benefits (i.e. high-quality paternal alleles in offspring), which requires female infidelity to be heritable. Numerous studies have tested for a relationship between paternity success, or an offspring's paternity type (within-/extra-pair), and phenotypic traits signalling quality (in males or offspring, respectively), and have provided conflicting evidence. Very few studies, however, have quantified the additive genetic variance and heritability of (male and) female infidelity, impeding an accurate estimation of the force of selection on female infidelity via indirect additive genetic benefits. Using a 25-year genetic pedigree from a natural and isolated population of the Seychelles warbler (*Acrocephalus sechellensis*), a facultatively cooperative breeder known to be socially monogamous but genetically promiscuous, we assessed extra-group offspring production by females. We found non-zero additive genetic variance and heritability of female extra-group reproduction, but heritability was moderately small ($h^2 = 0.12$). Our results suggest that selection on female infidelity via indirect additive genetic benefits is unlikely to be strong and to play an important role in the evolution of female extra-group reproduction in this species.

4.2. Introduction

Extra-pair paternity (EPP), a direct consequence of infidelity, occurs frequently across socially monogamous taxa, yet the evolutionary forces underlying this behaviour remain elusive and highly debated (Griffith et al. 2002; Westneat and Stewart 2003; Forstmeier et al. 2014). In particular, given that infidelity can be costly for females and that, unlike for males, extra-pair fertilisations do not necessarily increase a female's reproductive success, it is unclear why females engage in extra-pair mating (Jennions and Petrie 2000).

Several hypotheses have been proposed to explain the evolution of female infidelity. Adaptive models maintain that infidelity has evolved under positive selection, as it improves female fitness either by limiting the costs of re-mating (i.e. in systems where males force copulations; Thornhill and Alcock 1983; Smuts and Smuts 1993) or by providing direct material benefits (e.g. fertility assurance, extra parental care or nutrients; Sheldon 1994; Birkhead 1995; Wedell 1997) or indirect genetic benefits (high quality, heterozygous or compatible genes in offspring; Hamilton and Zuk 1982; Watson 1991; Zeh and Zeh 1996; Brown 1997). Non-adaptive hypotheses, on the other hand, propose that infidelity does not increase female fitness and that it evolves because it is genetically correlated to traits under positive selection in males or females (Halliday and Arnold 1987; Arnqvist and Kirkpatrick 2005; Forstmeier et al. 2011; Forstmeier et al. 2014).

One of the most influential (adaptive) hypotheses on the evolution of infidelity is the 'good genes' hypothesis (Hamilton and Zuk 1982), which maintains that extra-pair fertilisations enable females to gain high-quality paternal genes in offspring (i.e. alleles that increase offspring fitness by additive genetic effect; Kempenaers 2007). In this scenario, the evolution of infidelity is hypothesised to be driven by selection acting through indirect additive genetic benefits and requires female infidelity to be heritable. A multitude of studies have assessed the good genes hypothesis by testing for a relationship between male traits signalling intrinsic quality (e.g. body condition and sexual ornaments) and male paternity (EPP and WPP) success, or by comparing the fitness components of within- *vs* extra-pair offspring. Such research has provided contrasting results (reviewed in e.g. Griffith et al. 2002; Ackay and Roughgarden 2007; Cleasby and Nakagawa 2012; Hsu et al. 2015). However, since gathering complete, accurate and long-term parentage data for natural populations is empirically challenging, the additive genetic and phenotypic variance (and covariance) components of EPP, and its heritability, in socially monogamous species have been rarely estimated (Reid et al. 2011a; Reid et al. 2011b; Reid, Arcese, and Losdat 2014; Reid, Arcese, Keller, et al. 2014; Reid and Wolak 2018).

Quantifying the narrow-sense heritability (i.e. the proportion of phenotypic variance explained by additive genetic effects) of female extra-pair reproduction should enable a more direct test of the good genes hypothesis, via an accurate estimation of the selection proposed to promote this behaviour (i.e. selection through indirect additive genetic benefits). In fact, the good genes hypothesis hinges on the idea that EPP displays high enough heritability (noting that the average heritability of mating behaviours across taxa is 0.35; Dochtermann et al. 2019) to cause a strong force of selection for female infidelity via indirect additive genetic benefits. This force of selection on female extra-pair reproduction, which can be measured as the likelihood that a female produces an extra-pair young (female EPP likelihood), can be described by the expression:

$$\Delta_I = h^2 * \sigma * d \qquad \textit{(Eqn 1)}$$

where Δ_I is the number of phenotypic standard deviations by which the mean frequency of EPP would evolve in one generation through this selection (i.e. via indirect additive genetic benefits), h^2 is the heritability of female EPP likelihood, σ is the phenotypic standard deviation of this likelihood and d is the difference in mean additive genetic fitness between extra-pair and within-pair offspring (Arnqvist and Kirkpatrick 2005; Reid et al. 2011b). To estimate the maximum value of Δ_I, a maximised phenotypic standard deviation can be calculated and used in *Eqn 1*: $\sigma_{max} = \sqrt{(\mu_{EPP}(1 - \mu_{EPP}))}$, where μ_{EPP} is the mean observed EPP rate across focal years in the population (Reid et al. 2011b). Given the multiplicative contribution of h^2, σ (or σ_{max}) and d to Δ_I, evidence of a zero or small h^2 (i.e. well below the average heritability of mating behaviours, $h^2 = 0.35$) suffices when assessing the contribution of indirect additive genetic benefits to the evolution of extra-pair reproduction (Reid et al. 2011b). Therefore, quantifying the additive genetic variance and heritability of female extra-pair reproduction is key if we are to understand whether this behaviour evolved via indirect additive genetic benefits to females.

Here, we analyse a 25-year genetic pedigree from the natural population of Seychelles warblers (*Acrocephalus sechellensis*) on Cousin Island (Republic of Seychelles). This species is socially monogamous but genetically promiscuous and is a facultative cooperative breeder. Given that >96% of birds have been individually colour-ringed and blood-sampled (for sexing and parentage assignment) since 1997 (Brouwer et al. 2010) and that inter-island migration is virtually absent (Komdeur et al. 2004; Komdeur et al. 2016), complete and accurate data on extra-group paternity is available for our study population. Using this data, we estimate the additive genetic variance and heritability of female extra-group reproduction. By doing so we hope to improve our understanding of the role that indirect additive genetic benefits may play in driving the evolution of female infidelity in a wild population.

4.3. Methods

4.3.1. Study system

The Seychelles warbler is an insectivorous passerine endemic to the Seychelles archipelago. The population residing on Cousin (29 ha, 04°20′S, 55°40′E) has been monitored as part of a long-term study, which started in 1981 and was intensified in 1997 (Komdeur 1992; Richardson et al. 2003; Hammers et al. 2019). Since then, virtually all breeding attempts have been followed each year during the major breeding season (June–September) and, often, also during the minor breeding season (January–March; Hammers et al. 2019) Every year, as many birds as possible were caught, either in the nest (nestlings) or using mist. Newly caught individuals were assigned a unique combination of three colour rings and a British Trust for Ornithology metal ring. Since 1997, over 96% of Seychelles warblers in the population have been ringed and blood sampled (*ca* 25 µl by brachial venepuncture) (Richardson et al. 2001). The DNA extracted from blood samples was used for molecular sexing (following Griffiths et al. 1998) and genotyping based on 30 microsatellite loci (see: Richardson et al. 2001; Spurgin et al. 2014). Parentage was assigned to 2039 offspring (born 1991-2018) using MasterBayes 2.52 (details in: Hadfield et al. 2006; Edwards et al. 2018) and served to construct a genetic pedigree (see: Edwards et al. 2018).

In the Seychelles warbler, inter-island dispersal is <0.1% (Komdeur et al. 2004; Komdeur et al. 2016) and individual re-sighting probability per season on Cousin is very high (*ca* 92–98%, Brouwer et al., 2010). Therefore, individuals that were not seen over two consecutive seasons could be safely assumed dead (Hammers et al. 2013) and accurate parentage data, not confounded by migration in and out of the population, was obtained.

Seychelles warblers are territorial: individuals normally pair up, reside in and defend the same territory for life (Komdeur 1992; Richardson et al. 2007). In about 30% (1997-1999) or 50% (2003-2014) of territories the dominant pair is joined by one or more subordinate of either sex (Komdeur 1992; Richardson et al. 2002; Richardson et al. 2007; Kingma et al. 2016). Each season, group membership and individual social status were assigned to all birds. Groups and their territory boundaries were identified using observed foraging and singing locations, non-aggressive social interactions and aggressive territorial interactions (e.g. Bebbington et al. 2017). Within groups, dominant pairs were identified via pair and courtship behaviours. Subordinate birds, which are often offspring that have delayed dispersal (Komdeur 1992; Kingma et al. 2016) were assigned ‘helper’ or ‘non-helper’ status based on their participation in offspring care (Komdeur 1994; Richardson et al. 2002).

Reproduction is seasonally limited by invertebrate availability and offspring are fed for an average of three months after hatching (Komdeur 1996a; Komdeur et al. 2016). Although Seychelles warblers are socially monogamous, *ca* 44% of offspring are sired by males other than the dominant male in their group (Richardson et al. 2001; Hadfield et al. 2006). We refer to dominant males as the 'social males' of reproductively mature females (dominant and subordinate) in their group, as males can reproduce with dominant and subordinate females in their territory. Clutches typically consist of one egg, though *ca* 20% of nests contain two or three eggs, often laid by subordinate females (Richardson et al. 2001). In fact, around 15% of offspring in the population are produced by subordinate females (Richardson et al. 2001). Almost all paternity (within and extra-pair) is acquired by dominant males (Richardson et al. 2001); only *ca* 2.5% of young are sired by subordinate males (usually those transitioning towards dominant status; H. Dugdale, unpublished data), and *ca* 0.9% of offspring are produced by within-group subordinate males (Raj Pant et al. 2019). Thus, EPP is almost always extra-group paternity (EGP), i.e. resulting from fertilizations by dominant males from outside the group (hence we will use the term 'EGP').

In the Seychelles warbler, extra-group offspring (EGO) are often sired by males from neighbouring territories (Richardson et al. 2001). The likelihood that females produce EGO, however, is not influenced by local (nor population-wide) breeding density and synchrony (Raj Pant et al. 2019). Females are more likely to produce EGO when living in larger groups and, for subordinate females only, when relatedness to the social male is higher, though this does not prevent inbreeding from occurring in the population (Raj Pant et al. 2019).

The annual production of EGO in both males and females is known to vary with age, increasing in early life and declining in late life (Raj Pant et al. under review; chapter 3). No between-individual differences in extra-group reproduction have been shown. This indicates that males of higher intrinsic quality (as indicated by longer life-span and/or earlier age of first dominance) do not produce more EGO each year (lack of evidence for indirect 'good genes' benefits of EGP; Raj Pant et al. in review; chapter 3). On the other hand, older research in the Seychelles warbler provided evidence for MHC-dependent EGP (Richardson et al. 2005) and a positive link between MHC diversity and juvenile survival, providing support for indirect benefits via heterozygosity (Brouwer et al. 2010).

4.3.2. Statistical analyses

We estimated the repeatability and heritability of the likelihood that females produced an extra-group offspring ('female EGP likelihood'), while controlling for factors that influence this probability: the age of the mother and her social male (Raj Pant et al. in review; chapter 3), group size – i.e. the number of independent birds (i.e. ≥3 months old) in the offspring's natal group – and social male identity (Raj Pant et al. 2019; chapter 2). We did not include a social male's MHC diversity in our models due to the paucity of MHC data (any effect of MHC diversity on EGP likelihood will thus be reflected by social male identity). We compiled a dataset comprising 1553 offspring of known parentage (assigned with confidence ≥ 0.8) born on Cousin between 1994 and 2018. The likelihood that an offspring resulted from an extra-group fertilization was measured for 455 females (across 25 years and 42 field periods) and was on average 40% (626/1553 offspring). We ran all statistical analyses on this dataset in R 3.5.3 using the package MCMCglmm 2.28 (Hadfield 2010). All models were built as generalised linear mixed models (GLMMs) with a binomial error structure (logit link; response variable: female EGP likelihood) and five non-collinear (VIF ≤ 3) fixed effects, which were standardised (mean-centred and scaled to one standard deviation): the linear and quadratic age of mothers and of their social males, and group size. All GLMMs included social male identity as one of the random effects. Given that the variance of the response variable was close to zero, we specified a parameter-expanded prior for all models: V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000 (Hadfield 2019). By convention, the residual variance was set to 1 in all GLMMs, because it cannot be independently estimated in binomial models where the mean defines the variance. The posterior distribution of all models was sampled every 1000 iterations, with a burn-in period of 50,000 and a run of 10,000,000 iterations. Convergence was assessed through time-series plots of model parameters and their effective sample sizes, autocorrelation values ($r < 0.1$) and the heidel.diag function. Power analyses (Morrisey and Wilson 2009) revealed that we had statistical power (≥ 0.8) to detect heritability values ≥ 0.26 (Supplementary Fig. S4.1).

First, we estimated the repeatability of female EGP likelihood (R_{EGP}) using the variance components extracted from a GLMM (model 1) with the following predictors: group size, the linear and quadratic age of mothers and of their social males (fixed effects), social male and female identity (random effects). The repeatability of female EGP likelihood was estimated on the latent (logit) scale as: $R_{EGP,lat} = V_I/(V_P + \pi^2/3)$, where V_I is the variance explained by female identity, which includes both additive genetic (V_A) and permanent environment (V_{PE}) effects (i.e. common environment effects); V_P is the total phenotypic variance, which is the sum of V_I, any other random effect variance (here, social male identity) and the residual variance

(V_R); the term $\pi^2/3$ is added because the logistic variance is proportional to it (Nakagawa and Schielzeth 2010). Repeatability was also estimated on the original scale as: $R_{EGP,ori} = (V_I P^2/(1 + \beta_0)^2)/((V_P)P^2)/(1 + \beta_0)^2 + P(1 - P))$, where $P = \exp(\beta_0)/(1+\exp(\beta_0))$, i.e. the inverse-logit transformation of the link-scale intercept β_0 (Nakagawa and Schielzeth 2010).

Second, we estimated the heritability of female EGP likelihood (h^2_{EGP}) by extending model 1 into animal models, models 2–5 (following Kruuk and Hadfield 2007). We progressively added the following random effects: (I) the animal term, linked to the pedigree (pruned to 698 informative females), to model V_A, now separated from V_{PE}, which is reflected by female identity (model 2); (II) the field period, nested within the year, to account for temporal effects (model 3); and, (III) the identity of each female's mother (i.e. the maternal grandmother of each female's extra-group/within-group offspring), to account for maternal effects. Given that for 435/1553 cases the identity of the female's mother was missing, we assigned a dummy maternal identity to each female with unknown mother (model 4). To test that this procedure did not bias results, we also analysed a subset (n = 1118) of offspring produced by females with known mothers (model 5). The heritability of female EGP likelihood was estimated on the latent (logit) scale as $h^2_{EGP,lat} = V_A/(V_P + \pi^2/3)$ and on the original scale as $h^2_{EGP,ori} = (V_A P^2/(1 + \beta_0)^2)/((V_P)P^2)/(1 + \beta_0)^2 + P(1 - P))$, where V_P is the sum of V_A, V_{PE}, other random effect variances and V_R (Nakagawa and Schielzeth 2010).

Finally, we evaluated the maximum strength of selection on female EGP likelihood via indirect additive genetic benefits, by multiplying the observed average female EGP likelihood in our population (μ_{EGP}) by the maximised phenotypic standard deviation (σ_{max}) in this likelihood, as *Eqn 1* (Arnqvist and Kirkpatrick 2005; Reid et al. 2011b).

4.4. Results

Female EGP likelihood had a significant but low repeatability ($R_{EGP,lat}$ = 0.12, $R_{EGP,ori}$ = 0.13, Table 4.1) – noting that the average repeatability for behavioural traits across taxa is 0.37 (Bell et al. 2009). It also had a significant between-female variance V_I (i.e. V_A plus V_{PE}), which accounted for *ca* 27% of the phenotypic variance in the repeatability GLMM (model 1; see Fig. 4.1, Table 4.1).

Female EGP likelihood had a significant, moderately small heritability: $h^2_{EGP,lat}$ = 0.13 and $h^2_{EGP,ori}$ = 0.12 (Table 4.2), noting that the average heritability of behavioural traits across taxa is 0.24 (Dochtermann et al. 2019). Disentangling V_A from V_{PE} (in the animal models) revealed that virtually all V_I reflected significant additive genetic effects, which explained 28% of phenotypic variance in female EGP likelihood, while permanent environment effects explained near-zero variance (Fig. 4.1, Table 4.2).

Year and field period explained near-zero variance in female EGP likelihood. Maternal effects also explained near-zero variance, both in model 4 (fitted on the full dataset, using a dummy variable when the identity of a female's mother was missing) and in model 5 (fitted on a subset of females with known mothers), which indicates that our dummy variable procedure did not bias results (Table 4.2, Supplementary Table S4.1). Consistent with previous research in the Seychelles warbler, social male identity explained a large amount (41%) of variance in female EGP likelihood and all fitted fixed effects (group size, female and social male age and age^2) had a significant influence on EGP likelihood (Fig.4.1-4.2).

To assess the strength of selection via indirect additive genetic benefits on female extra-pair reproduction (without accounting for any differences in additive genetic fitness between EGO and WGO), we multiplied the heritability of female EGP likelihood by the maximised phenotypic standard deviation in this likelihood. The multiplicative value obtained was small (0.059): $\Delta_I = h^2 * \sigma_{max} * d = 0.12 * 0.49 * d = 0.059 * d$, where $\sigma_{max} = \sqrt{0.40(1 - 0.40)}$ and 0.40 is the observed female EGP likelihood in our study population.

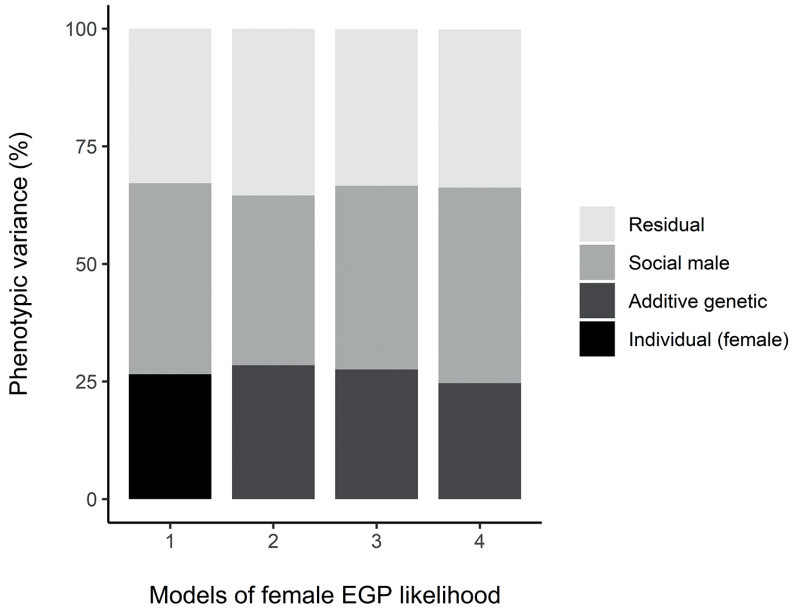


Figure 4.1. Variance components of the likelihood that female Seychelles warblers produce an extra-group offspring ('female EGP likelihood'), from our GLMMs (Table 4.1). In model 1, the individual variance consists of the additive genetic (V_A) plus the permanent environment (V_{PE}) variance; in models 2-4 (animal models), V_A and V_{PE} are modelled separately (V_{PE} is not visible in the figure as it explains < 0.1% of the total phenotypic variance). Year and field period (models 3–4) and the maternal effect (model 4) do not appear in the figure as they explain < 0.1% of the total phenotypic variance.

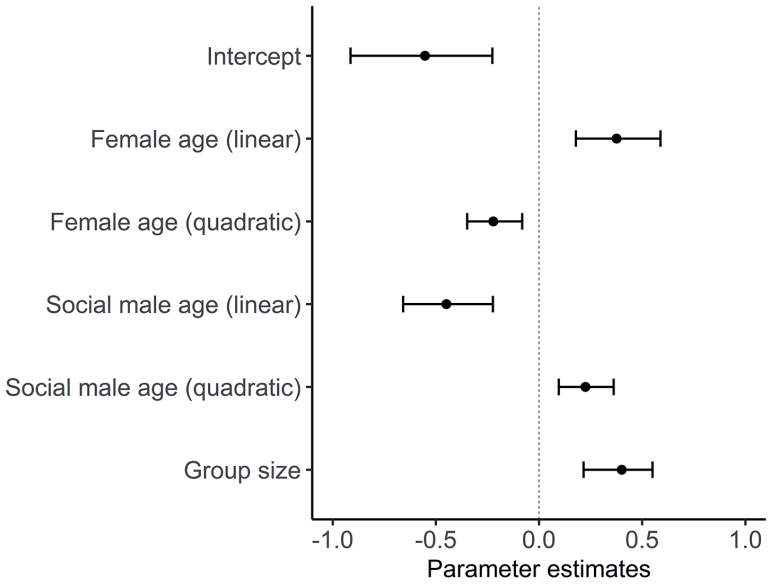


Figure 4.2. Effect of female age, social male age and group size on the likelihood that females Seychelles warblers produce an extra-group offspring. The posterior modes of fixed effects from our full GLMM (model 4, see Table 4.2) are plotted with their associated 95% credible intervals (error bars). All parameters are significant (i.e. have credible intervals not overlapping zero).

Table 4.1. Posterior modes (and 95% credible intervals) of variance components and repeatability estimates from GLMM 1 (response variable: likelihood that a female Seychelles warbler produces an extra-group offspring; fixed effects: group size, female and social male age). Residual variance is set to 1. V_I = individual female variance, $R_{EGP,lat}$ = latent-scale repeatability, $R_{EGP,ori}$ = original-scale repeatability.

Model	V_I	Social male	$R_{EGP,lat}$	$R_{EGP,ori}$
1	0.81	1.23	0.12	0.13
	(0.15 - 1.53)	(0.55 - 2.02)	(0.03 - 0.23)	(0.03 - 0.23)

Table 4.2. Posterior modes (and 95% credible intervals) of variance components and heritability estimates from GLMMs 2-4 (response variable: likelihood that a female Seychelles warbler produces an extra-group offspring; fixed effects: group size, female and social male age). GLMMs have a progressively higher number of random terms. The residual variance is set to 1. V_A = additive genetic variance, V_{PE} = permanent environment variance, $h^2_{EGP,lat}$ = latent-scale heritability, $h^2_{EGP,ori}$ = original-scale heritability.

Model	V_A	V_{PE}	Social male	Year	Field period	Maternal effect	$h^2_{EGP,lat}$	$h^2_{EGP,ori}$
2	0.80	< 0.001	1.02	-	-	-	0.13	0.10
	(0.21, 1.66)	(< 0.001, 0.63)	(0.52, 1.93)				(0.04, 0.24)	(0.04, 0.21)
3	0.83	0.004	1.17	< 0.001	< 0.001	-	0.12	0.11
	(0.19, 1.65)	(< 0.001, 0.64)	(0.52, 1.93)	(< 0.001, 0.06)	(< 0.001, 0.06)		(0.04, 0.24)	(0.03, 0.21)
4	0.73	0.001	1.24	< 0.001	< 0.001	0.003	0.13	0.12
	(0.12, 1.61)	(< 0.001, 0.62)	(0.49, 1.93)	(< 0.001, 0.06)	(< 0.001, 0.06)	(< 0.001, 0.52)	(0.02, 0.23)	(0.02, 0.19)

4.5. Discussion

In Seychelles warblers, the likelihood that the (normally single) offspring produced in a clutch by a female was an EGO (on average 40%) showed low repeatability (R = 0.13) and moderately low heritability (h^2 = 0.12). The additive genetic variance (V_A) comprised a significant amount (24%) of the total phenotypic variance in this likelihood, while the permanent environment variance (V_{PE}) was near-zero. This suggests that the between-individual variation in female EGP likelihood is largely driven by additive genetic effects and not by common environment effects.

The heritability of female EGP likelihood in the Seychelles warbler was about half the size of the average heritability of behavioural traits (h^2 = 0.24) and less than half the size of the mean heritability of mating behaviours (h^2 = 0.35) across taxa (Dochtermann et al. 2019). It was in the low end of the range of the heritability spectrum for behaviours in other species (Dochtermann et al. 2019) and close to that of a personality trait (h^2 = 0.17, exploratory behaviour) in the Seychelles warbler (Edwards et al. 2017). Female EGP likelihood in Seychelles warblers showed a similar heritability to female EPP rate (Reid et al. 2011b) and EPP likelihood (Reid 2012; Reid, Arcese, Keller, et al. 2014) in a natural population of the song sparrow (*Melospiza melodia*) and to female EPP rate in a captive population of the zebra finch (*Taeniopygia guttata*; Forstmeier et al. 2011). To our knowledge, the aforementioned song sparrow studies are the only ones that have quantified the V_A and heritability of female extra-pair offspring production in a socially monogamous natural population (see also: Reid and Wolak 2018). More (though still few) studies to date have calculated the narrow-sense heritability of polyandry, in terms of multi-male mating by females, in promiscuous species (more commonly in lab systems) and have also provided moderately low heritability estimates (see e.g. Simmons 2003; Shuker et al. 2007; Evans and Simmons 2008; McFarlane et al. 2011).

One of the key hypothesis on the evolution of infidelity, the good genes hypothesis, maintains that female infidelity evolved under selection acting through indirect additive genetic benefits, i.e. enhanced (additive) genetic quality, and thus lifetime reproductive success, of extra-pair offspring (Hamilton and Zuk 1982). In order for female infidelity to evolve via this indirect selection, female extra-pair reproduction is required to show V_A and h^2 greater than zero (Arnqvist and Kirkpatrick 2005; Reid et al. 2011b). In the Seychelles warblers this is true, but the heritability of female EGP likelihood is moderately low, which suggests that the strength of selection via 'good genes' benefits (Δ_I) is unlikely to be high. In fact, the posterior mode, and even the upper 95% credible interval estimate, of h^2 in our study are lower than assumed

heritability values (0.4 or 1.00) used in published estimations of the maximum possible Δ_I, which was found to be small (see: Arnqvist and Kirkpatrick 2005). Moreover, we find that the product of the heritability and the maximised phenotypic standard deviation (0.49) in female EGP likelihood is also small (0.059), further suggesting that Δ_I is unlikely to be strong in the Seychelles warbler.

For Δ_I to be high, the difference between the additive genetic value of EGO and WGO (d) is required to be considerable. To date, evidence that extra-pair young are fitter than their within-pair maternal half-sibs is scarce (Arnqvist and Kirkpatrick 2005; Ackay and Roughgarden 2007). No differences in or, even, lower fitness levels of extra- *vs* within-pair young have emerged from numerous studies assessing offspring fitness components (or traits hypothesised to correlate with fitness) in specific life-history stages (e.g. Krokene 1998; Whittingham et al. 2001; but see e.g. Foerster et al. 2003) or, more reliably, throughout life (e.g. Sardell et al. 2012; Hsu et al. 2014) (but see e.g. Schmoll et al. 2009). Notably, a limitation of these studies is that they assess the phenotypic fitness of offspring, which mirrors both genetic and environmental effects. Moreover, fitness comparisons of within- and extra-pair offspring do not strictly test whether extra-pair offspring are fitter than the within-pair offspring that a female would have produced had she only copulated with her social male (i.e. the true assumption of indirect genetic benefit models). To our knowledge, only one study has performed such a comparison, availing itself of an extensive pedigree from a natural population of song sparrows (Reid and Sardell 2012). This study estimated the additive genetic value for recruitment (i.e. the sum of the average additive effect of an individual's alleles on recruitment) of the extra-pair offspring and their hypothetical within-pair siblings. Reid and Sardell (2012) found that extra-pair offspring had lower additive genetic value for recruitment and suggested that there may be a (weak) indirect selection against female extra-pair reproduction in the song sparrow.

In the Seychelles warblers, previous work has shown that females paired with males carrying low MHC diversity were more likely to obtain extra-pair fertilisations with males of higher MHC diversity (Richardson et al. 2005), and that juvenile survival was predicted by MHC diversity (Brouwer et al. 2010). These findings suggest that extra-pair offspring may be fitter than the within-pair offspring that they have substituted, and that this fitness difference is due to (over-)dominance genetic effects (heterozygous advantage). Whether within- and extra-pair offspring differ in their additive genetic fitness is however not yet known. In any case, the moderately low heritability of female extra-pair reproduction, suggests that the force of selection via indirect additive genetic benefits is unlikely to be strong.

Although we cannot completely exclude that the evolution of female infidelity is partially driven by good genes benefits, it is more likely that other mechanisms are responsible. Given that female extra-pair reproduction shows non-zero heritability, there seems to be potential for a continued response to selection on this female trait (Reid et al. 2011b). Such selection may be indirect and promote female extra-pair reproduction through non-additive genetic benefits, such as heterozygosity or genetic compatibility in offspring (Zeh and Zeh 1996; Brown 1997), which would increase fitness via epistasis, dominance or over-dominance (see: Kempenaers 2007). Alternatively, there could be selection on female infidelity acting via direct benefits to polyandrous females, e.g. fertility assurance (Sheldon 1994); further research is needed to investigate this in the Seychelles warbler.

Another possibility is that infidelity is not adaptive to females and that it evolved because of genetic constraints (Halliday and Arnold 1987; Arnqvist and Kirkpatrick 2005). Female infidelity may have co-evolved under sexually-antagonistic selection with traits improving male reproductive competitiveness (Halliday and Arnold 1987; Keller and Reeve 1995; Arnqvist and Kirkpatrick 2005). This may occur either via linkage disequilibrium deriving from assortative mating between unfaithful females and successful sires (Keller and Reeve 1995) or via pleiotropic effects between alleles carrying female infidelity and alleles carrying male traits that increase paternity success (Halliday and Arnold 1987). Very few studies to date have tested such hypotheses in socially monogamous species and have mostly failed to provide clear supporting evidence (Reid, Arcese, Keller, et al. 2014; Zietsch et al. 2015; Reid and Wolak 2018) (but see: Forstmeier et al. 2011). Alternatively, female infidelity may have evolved because genetically correlated to female traits enhancing reproductive success (Arnqvist and Kirkpatrick 2005; Forstmeier 2007). To our knowledge, only two studies have quantified the genetic correlation between female infidelity and a traits increasing reproductive success in socially monogamous species and have both produced no clear evidence for this (Forstmeier et al. 2011; Reid 2012). More studies are needed to quantify variance and covariance components of female infidelity if we are to fully understand the genetic mechanisms underlying the evolution of this mating behaviour.

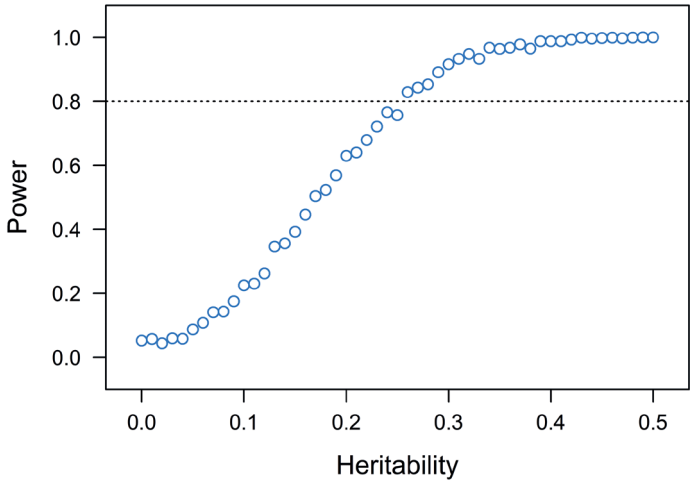
4.6. Conclusions

Our study is one of very few to directly address a genetic mechanism potentially underlying the evolution of infidelity in a socially monogamous system. We quantified the additive genetic variance and heritability of female infidelity, and showed that these genetic measures are non-zero, but that heritability is moderately low in the Seychelles warbler. Our findings undermine the influential 'good genes' hypothesis, which maintains that female infidelity evolved because of selection acting via indirect additive genetic benefits. Our results suggest that female extra-pair reproduction may evolve via other (non-additive) indirect genetic benefits (i.e. heterozygosity/genetic compatibility), direct benefits (e.g. fertility assurance), or due to genetic constraints (i.e. within- or cross-sex genetic correlations with other traits under positive selection).

4.7. Supplementary material

Supplementary Table S4.1. Posterior modes (and 95% credible intervals) of variance components and heritability estimates from GLMM 5 (response variable: likelihood that a female Seychelles warbler produces an extra-group offspring; fixed effects: group size, female and social male age). The residual variance is set to 1. V_A = additive genetic variance, V_{PE} = permanent environment variance, $h^2_{EGP,lat}$ = latent-scale heritability, $h^2_{EGP,ori}$ = original-scale heritability.

Model	V_A	V_{PE}	Social male	Year	Field period	Maternal effect	$h^2_{EGP,lat}$	$h^2_{EGP,ori}$
5	1.05	0.01	0.67	< 0.001	0.001	0.004	0.17	0.14
	(0.19, 2.52)	(< 0.001, 1.06)	(< 0.001, 1.61)	(< 0.001, 0.11)	(< 0.001, 0.13)	(< 0.001, 0.70)	(0.04, 0.33)	(0.03, 0.30)



Supplementary Figure S4.1. Plot of heritability values (for the likelihood of producing extra-group offspring) and associated detection power in female Seychelles warblers.